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Distribution of polysaccharides within the humic compounds of soils subjected to a humivorous termite *Thoracotermes macrothorax* Sjöstedt

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Summary. *Thoracothermes macrothorax* Sjöstedt, a humivorous termite, has a positive influence on the stuctural stability of soils by including its faeces (laden with stable organo-mineral micro-aggregates) in all of its constructions (nest and underground galleries). The observation of a high contents of polysaccharides in soil humic compounds (especially in the humin fraction of organic carbon) under the influence of this species could prove one of the factors which helps to maintain that stability.

Key words: Tropical soils, humic compounds, polysaccharides, humivorous termites

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Introduction

Throughout tropical ecosystems, and particularly in rain forests, termites play a major role in the breakdown and transformation of organic matter (Lee & Wood 1971; Lepage 1972, Garnier-Sillam 1987; Okwakol 1987; Lal 1988).

However, the different termite species are involved at various stages along the trophic chains, and their effect, very diversified on the degradation of the vegetal energetic supply within the ecosystem, cannot be generalised. Among Termitidae, humivorous termites, which generally feed off soil humus, stand quite apart. *Thoracotermes macrothorax* Sjösted (Termitidae, Termitinae) builds up a termitary whose club-shaped epigeous part is two feet high, the nest pediment being approximately 4 inches below ground level, with adjoining large cavities (3 to 6 cms in diametre) from which subterraneous horizontal galleries (périécle: Grasse 1984) branch away. Worker termites remove their building materials from the humiferous horizons laden with compounded forms of both mineral and organic matter. As with most humivorous species, they use the pasty contents from their posterior gut to buttress their constructions as well as to line up the internal walls of their chambers within the nest (Noirot 1970; Grasse 1984).

Our previous work has already shown the beneficial role played by *T. macrothorax* upon the organic cycle of soils while contributing to their preservation: by their coeval ingestion of both clay particles and vegetal debris, these termites, during gut transit, generate stable organo-mineral microaggregates that they reincorporate in every construction (Garnier-Sillam et al. 1985, 1986).

Both nest and surrounding soils directly subjected to the action of *T. macrothorax*, in contrast with control horizons, showed, viz: – an increase of organic carbon – a net increase of the humic compound contents, that is characteristic of a significant polymerisation of organic matter (Garnier-Sillam et al. 1989) – and a better structural stability (Garnier-Sillam et al. 1988).

In order to specify the particular action which humivourous termites exert on soils, we have carried out assays of polysaccharidic distribution in the humic compounds of samples submitted to termitic effect. Our aim was to determine whether or not the action of these macromolecules could be considered as one of the prevailing factors contributing to structural stability of termite-worked soils.

Materials and Methods

Definition

In this study, the following polysaccharide definition was used: Polysaccharides are polymers with a high molecular weight, elaborated from simple sugars (monosaccharides), amino-sugars and uronic acids (Stevenson 1973; Flaig 1975; Cheshire et al. 1992). This definition exemplifies the very heterogeneous structure of polysaccharides, due to both methodological and terminological problems. Hitherto, there is no such global method as to prompt a comprehensive assay of glucidic compounds. Since hexoses represent the most significant ratio of the sugars obtained through polysaccharide hydrolysis, we have opted for the method developed by Brinck et al. (1960) by using anthrone as a reactive dye that reacts with hexose-like sugars, i.e., with methylhexose and 6-deoxyhexose.
By means of such a colorimetric method which refers to a glucosic solute pattern, an important proportion of total polysaccharides can be obtained, therefore permitting the characterisation of several samples and a comparison between them (pentoses are not taken into account). Hence the term "polysaccharide" is used in this study as anthrone-assayed sugars, according to Brinck et al. (1960) and Guckert (1972) these relative values being relevant to the total soil polysaccharides.

Polysaccharide assay

Sulfuric hydrolysis and hydrolysate recovery: a sample, corresponding to 50 mg of carbon is reflux-hydrolysed in a 25 ml H_2SO_4 (N) solution during 6 hours. Once cooled off, hydrolysates are recovered by centrifugation and ultrafiltration.

Table 1. Analytical data for the samples (n = 4, S: sum of exchangeable cations; T: cation exchange capacity, V: saturation rate)

	Control topsoils (0–8 cm)	Topsoils (0–8 cm)	Nest walls	Faeces
		Thoracotermes macrothorax		
Particle size distribution (%)				
Clay	38.4	33.8	33.7	–
Fine silts	12.0	12.2	15.3	–
Coarse silts	16.0	18.3	13.9	–
Fine sands	10.4	16.3	9.8	–
Coarse sands	23.2	19.4	27.3	–
Chemical properties				
Organic carbon (‰)	27.8	46.4	40.0	85.8
Total nitrogen (‰)	2.23	3.87	3.62	10.85
C/N	12.46	11.98	11.04	7.90
pH (H_2O)	3.9	4.2	4.3	–
S (me/100 g)	0.84	1.51	1.57	–
CEC = T	15.0	21.4	19.1	–
S/T = V%	6.62	7.0	8.2	–
Total iron (g/100 g dry soil)	3.79	5.04	5.23	–
Exchangeable iron (g/100 g dry soil)	2.80	4.07	4.13	–
Total aluminium (g/100 g dry soil)	5.46	6.22	6.42	–
Exchangeable Al (g/100 g dry soil)	0.56	0.71	0.75	–
Total phosphorus (‰)	0.229	0.544	0.512	–

Colorimetric assay of polysaccharides: anthrone colorimetry (Brinck et al. 1960): an assay of the hydrolysis-derived reducing sugars. The glucosic contents of the solutions worth assaying are measured by relating their D.O. (625 mm) to the reference curve of glucose.

The assays have been carried out with whole samples, viz: – control humus sampled at 40 metres from the nest (taken from the first 8 cms of surface soil), – humus sampled at 30 cms from the nest (again, the first 8 cms taken from the surface soil), – nest walls, – *T. macrothorax* faeces – and on the different humic fractions of each sample. The results of humic extractions (extracted through pyrophosphate and soda, Bruckert et al. 1974; Dabin 1976) have been already published (Garnier-Sillam et al. 1989). Here, the results are averaged against the duplicated analysis of four different termite nests.

Analytical characteristics of the samples

The main analytical features of samples have already been accounted for (Garnier-Sillam et al. 1989, 1991) and have been recalled in Table 1. The samples come from the Mayombe forest (4°14 S, 12°26 E-Congo), the soils of which are classified as "upturned ferrallitic soils, with little events" (Jamet 1979).

Results

A comparative study of polysaccharide content in whole samples

A preliminary assay of polysaccharides has been performed on whole samples (Table 2) with a view to drawing up comparisons and possibly to highlighting various factors which favour glucidic compounds with reference to the analytical in Table 1.

It is worth noting that the polysaccharide contents varied to a great extent. The control soil shows a polysaccharide rate of 320 mg/100 g of soil whereas the rate of the *T. macrothorax*-worked humus was twice as much.

However, the ratios of polysaccharide content vs. overall organic carbon, oscillate between 11.51 to 14.02 for the soil samples, and we may surmise that the polysaccharide contents are directly in keeping with the rates of organic matter produced.

Nest walls also happen to exhibit a certain amount of polysaccharides (419.8 mg) in keeping with carbon contents (ratio: 10.49).

T. macrothorax faeces show a polysaccharide content of 975.2 mg/100 g of faeces. Here, the carbon content is significantly higher than that from the horizon on which the species feeds. However, the ratio 11, 36 shows that the polysaccharide proportion is closely related to the carbon content, while a smaller proportion might be expected because a part of glucidic compound, being quickly assimilated, will have been metabolised by the termite during gut transit.

Distribution of polysaccharides in the humic compounds

Table 2 recalls the carbon distribution in the three humic sections of samples (Garnier-Sillam et al. 1989). Only the humus worked by *T. macrothorax*, and its nest wall, can offer a FA/HA ratio of organic carbon significantly equal or inferior to 1 (1.08 and 0.86), whereas the other samples point to the prevalence of fulvic acids (control topsoils: 1.86, faces: 1.91). It is worth noting the high content of carbon found in the faecal humin of this particular termite, that uncertainly corresponds to a fresh organic matter unable to be extracted through pyrophoshate and soda (Garnier-Sillam 1987).

To get a thourougly detailed view of the various patterns of polysaccharides in every humic section, and to facilitate comparisons between several samples, the polysaccharide contents (a.v.) and their ratios with organic carbon in fulvic acids (FA), humic acids (HA) and humin (H) are presented on Table 2. The relative values (r.v.) of polysaccharide and carbon distributions are showed in Fig. 1.

Table 2. A comparative study of polysaccharide content in global samples and humic portions (averages ± standard deviation; n = 8; C: carbon; H.: humin)

	Control topsoils (0–8 cm)	Topsoils (0–8 cm)	Nest walls	Faeces
		Thoracotermes macrothorax		
Organic contents in humic portions (g/100 g dry soil) (Garnier-Sillam et al. 1989)				
Fulvic acids (FA)	1.08 ± 0.05	1.58 ± 0.06	1.28 ± 0.04	1.80 ± 0.06
Humic acids (HA)	0.58 ± 0.03	1.46 ± 0.07	1.48 ± 0.06	0.94 ± 0.08
Humin (H)	1.12 ± 0.06	1.60 ± 0.06	1.24 ± 0.05	5.84 ± 0.06
FA/HA (organic carbon)	1.86	1.08	0.86	1.91
Polysaccharide contents				
(mg/100 g dry soil)	320.0 ± 22.2	650.7 ± 32.4	419.8 ± 37.1	975.2 ± 45.6
Polys C/total C (× 100)	11.51	14.02	10.49	11.36
Polysaccharide contents in humic proportions (mg/C100g dry soil)				
Fulvic acids (FA)	87.0 ± 8.6	135.3 ± 15.3	60.8 ± 6.5	218.8 ± 19.2
Humic acids (HA)	19.5 ± 2.3	67.7 ± 6.4	53.9 ± 5.3	33.3 ± 4.3
Humin (H)	213.5 ± 21.3	447.7 ± 32.1	305.1 ± 23.6	723.1 ± 45.6
Polysaccharides C/humic fractions C (× 100)				
Fraction fulvic acids	8.0	8.5	4.7	12.1
Fraction humic acids	3.3	4.7	3.7	3.5
Fraction Humin	19.0	27.0	24.6	12.4
Fraction FA/Fraction HA	2.42	1.80	1.27	3.45

Distribution of polysaccharides in fulvic acids and humic acids: extractible organic compounds (FA and HA) present a net distribution variation, with a marked predominance of polysaccharides in fulvic acids vs. humic acids in both humus (27% of FA and 6% of HA in the control soils, 21% of FA and 10% of HA in *T. macrothorax* humus) and faeces (23% of FA and 3% of HA). FA/HA ratios derived from comparing polysaccharide rates in each humic fraction can be presented as follows: control humus = 2.42; *T. macrothorax* humus = 1.80; faeces = 3.45. Now, as far as the nest wall is concerned, even though the HA organic carbon content exceeds in absolute value the FA one, the polysaccharide rate

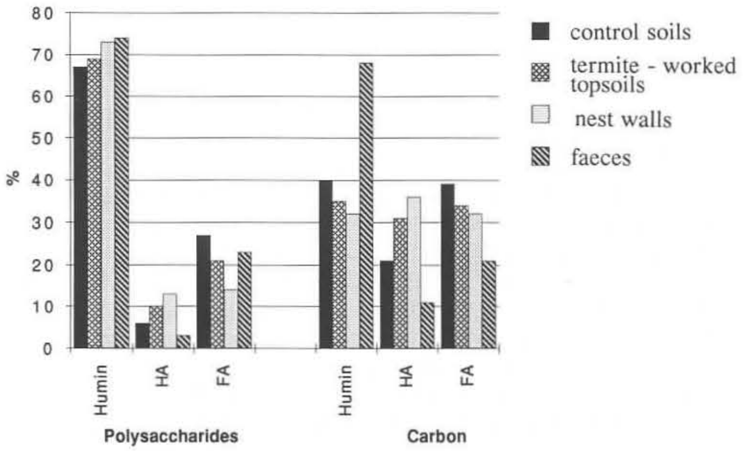

Fig. 1. Distribution of polysaccharide and organic carbon contents in the humic compounds (relative values)

turns out to be more important in fulvic acids than in humic acids (FA/HA of organic carbon = 0.86 and FA/HA of polysaccharide humic fractions = 1.27). The ratio between polysaccharide content and total organic carbon in every HA fraction in all four samples exhibits a somewhat weak variation of amplitude (3.3 to 4.7), which remains lower in the FA ratio (4.7 to 12.1); still, for the nest wall, the polysaccharide amount for FA (60.8 mg/100 g dry soil, ratio of 4.7) is very slightly higher than for HA (53.9 mg/100 g dry soil, ratio of 3.7).

Distribution of polysaccharides in the humin fraction: a basic opposition is noticed between organic matter (FA + HA) when solubilised by alkine reagents and non-extractible organic compounds which make up humin since, quite paradoxically, polysaccharides – known to be thoroughly fermentable and evanescent compounds – turn out to be mostly non-soluble for the stable fraction of the organic matter.

For the given four samples, indeed, the highest sugar rates were found in humin (Table 2; Fig. 1). For an absolute value, the high polysaccharide content in the *T. macrothorax* humus (447.7 mg) relative to the humus control (213.5 mg) must be paralleled with the humin carbon content of this horizon.

The humin polysaccharidic contents vs. the carbon hydrate count (Table 2) which have been assayed in the four samples, clearly show higher values in the two termite-worked soil samples (respectively 447.7 mg/100 g dry soil (69%) in *T. macrothorax* humus and 305.1 mg/100 dry soil (73%) in the nest walls). *T. macrothorax* faeces, for an absolute values, are themselves laden with a high polysaccharide content, the percentage of which is about 74% in humin (723.1 mg/100 g dry soil), the remainder being more properly localised in the FA 23% (218.8 mg/100 g dry soil). The result suggests that the feeding needs of *T. macrothorax* are made on a less polymerised vegetal matter than the one to be normally found in humus.

Discussion and Conclusion

In our study, the polysaccharide contents oscillate between 10.46 to 14.02% of organic carbon. These results are in agreement with several authors (Schnitzer & Khan 1972; Guckert 1973; Cheshire et al. 1992) rather think that glucids amount to 5 to 25% of soil organic matter. Moreover, superficial horizons do sustain an active telluric microflora (bacterial or fungal) whose polysaccharidic secretive outputs exert an influence on the global value of carbohydrates (Anderson 1989).

The subsequent results of our present study show:

1. Significant proportions of polysaccharides in the samples subjected to termitic action

In the faeces, the carbon content is significantly higher than that from the horizon in which the species feeds. The result we obtained bears out the notion of a selective intake of vegetal compounds (Garnier-Sillam 1987) practised by this termite.

In most of the samples, the polysaccharides can be said to stem from the biodegradation of the vegetal organic matter. In so far as faeces are concerned, gut-secreted polysaccharides are paramount; they are to be found, hereafter, in the topsoil worked by termites and in their nest wall because, by their biological behaviour, humiferous termites incorporated their own faeces in all their constructions. Amid these areas and artifacts come also saliva-excreted polysaccharides; actually, during nest-making. *T. macrothorax* uses cibarial earth pellets too. Now as regards termite-worked humus, elektron microscopy enabled us to highlight an active telluric microflora thriving under favourable pedoclimatic conditions (i.e. with high carbon contents) and thus a significant rise of microbial polysaccharides would ensue (Garnier-Sillam 1987).

Thus, termitic biological activities can be said to raise the polysaccharide output in the termitary-dominant area.

For the polysaccharides found in extractable organic compounds, the assays practised on humic compounds have brought to light that the important amount of humic acids, as recorded in humivorous termite-worked humus, pinpoint a high polymerisation of organic matter and surely contribute to the making of humic-clay complexes of the soil (Garnier-Sillan et al. 1989). An electron-microscope scanning of faecal humin samples shows a certain amount of organo-mineral bonds persiting after alkaline extraction of the humic cementing agents, which emphasizes their stability (Garnier-Sillam 1987).

Extractable organic compounds (FA and HA) present a net distribution variation, with a marked predominance of polysaccharides in fulvic acids vs. humic acids in both humus and faeces. To a certain degree, polysaccharides are, indeed, nothing less than soil-deposited metabolites after the biodegradation of vegetal debris from the termite litter; hence the normal higher proportion of these compounds found in the fulvic acids, which can be partly considered as precursors of stable humic compound. It appears, therefore, that the reduction of polysaccharidic chains depends on the state of evolution of organic matter. The results suggest that the HA broadly correspond to condensed molecules in which polysaccharides play but a minor role in the form of lateral chains (Barrioso et al. 1985).

2. *Important rates of polysaccharides in the humin of samples influenced by termites*

Paradoxically polysaccharides that are insolubilizable short-lived compounds are mostly found in the stable fraction of the organic matter, namely humin. For the given samples, indeed, the highest sugar ratios were found in humin. Something which enhances the signal role played by polysaccharides in humin has already been observed in temperate soils by Dormaar (1967), Guckert (1973) and Cheshire et al. (1973).

Consistently with increasing carbon rates greater polysaccharidic supplies are observed in humin in cations-enriched samples and denser in humic compounds (termite worked topsoils and nest walls) were on the other hand organo-mineral blends are much more favoured than in the control humus (Garnier-Sillam et al. 1989).

The result allows a discussion of the very nature of the mechanisms which trigger the incorporation of glucidic compounds into that fraction of organic matter. Humin organic matter* is found to be mostly trapped within mineral constructions. Therefore, polysaccharides are neoformed as microbial residual compounds, released after hydrolysis of the trapped organic matter.

The high content of polysaccharides as recorded *T. macrothorax* humin topsoil – and compared with that of the control humus – may stem from a fast input of neoformed carbon hydrates in stabilised organic matter. In such a case, we might think, along with Duchaufour (1979), that an insolubilising humin builds up, after early polysaccharidic binding with the mineral fraction, which would somehow bring humin to a certain maturing phase during which neutral sugars partly evolve towards more stable compounds, say, into osamine types. Then, an alteration of the lateral chains of humified compounds would occur, as generated by condensation of certain simple sugars with amino-acids, to yield eventually amino-polysaccharides. Likewise, certain stable bonds between polysaccharides and phenol acids can be assumed (Guckert 1972).

Both types of compounds (amino-polysaccharide and polyphenol complexes) have a higher resistance to biodegradation than plain polysaccharides, as demonstrated by Gallali (1972) or Griffiths & Burns (1972). By undergoing such processes, glucidic compounds, though remaining somewhat labile, do manage to merge with the humin fraction, thereby being granted an important stability.

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* **A recap:** humin (Duchaufour 1983). Pyrophosphate extraction proving useless to sort out fresh organic matter from inherited humin and from a really humified organic matter, humin here is synonymous with unextractable carbon, regardless of its nature (insoluble humin, microbial humin, inherited humin, or vegetal debris surrounded with phylliteous minerals.) Humin, therefore, represents the non-extractable organo-mineral fraction in an alkaline medium, on two counts: – chemical insolubility of biomass right from the start (inherited humin) or through a gradual condensed stage until functional groups are lost (condensation humin) – molecular adsorption onto mineral supports (organo-mineral complexes) the very size and nature of which are important in these interactions.

On the other hand, humin polysaccharides may partly result from the relative immobilisation of hydrosoluble glucidic products originating from the termites' litter, after salt build-ups or complexes formed with metallic cations. Actually, Saini (1966) and Martin (1971) have shown that polysaccharides are able to build up salts with metallic ions, whose reaction prevents a possible polysaccharidic hydrolysis by microbial enzymes. Furtermore, the very fact that polysaccharides, in the main, can withstand an alkaline extracting reagents (sodium pyrophosphate + soda) allows them to form important stable bonds with clays; the presence of mineral colloids would then ensure, as one of the determining factors, the maintainance of polysaccharide in humin.

To conclude: the content of polysaccharides may be closely related to certain analytical data, viz: (*1*) to organic matter ratios, hence to a pronounced biological activity (more appropriately) of a termitic origin in our study – but also to the presence of a certain amount of mineralogic clay (*2*) to exchangeable cation rates, in particular calcium and potassium cations which span organic colloids and mineral surfaces (*3*) to exchangeable properties as directly connected with organic matter and clay proportions.

A preferential localication in humin of polysaccharides from residual neoformed and microbial compounds allows us to hypothesis important bonds between sugars and clay, which would favourable establish and influence upon the stability of micro-aggregates in the humiferous horizon worked by *T. macrothorax*.

Such a result, contributing to the framework of studies as reviewed in our introduction, enables us to ascertain that the biological activity of the humivorous termite *T. macrothorax* has a beneficial role towards the sustained fertility of tropical forest soils.

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